

But one question remains unanswered: is there correspondence between the motion-induced blindness-related BOLD modulations observed in human and in monkey area V1? Donner *et al.* [5] observed a global but no target-specific modulation (that is, activation stronger in target than in non-target voxels) in human V1, whereas Maier *et al.* [4], who did not compare target with non-target voxels, could not draw this distinction. Perhaps, then, the motion induced blindness-related BOLD modulations in monkey V1 are global in nature and, therefore, present within retinotopic regions of V1 well beyond the target representation.

So, thanks to the potent, intermittent perceptual suppression of vision induced by motion induced blindness, we are beginning to see how different components of neural responses within the visual hierarchy are related to fluctuations in visual perception, and we can expect to learn even more about the neural concomitants of motion induced blindness in the near future [7,8]. Moreover, we are beginning to witness some convergence between the results of monkey neurophysiology and human brain imaging in situations where perception and physical stimulation are dissociated.

It would be gratifying if the same convergence could be realized in the case of binocular rivalry, another compelling phenomenon in which visual awareness fluctuates even though physical stimulation remains invariant [2]. In the rivalry literature, there are nagging inconsistencies between human brain imaging results and monkey single-cell results, but no one has yet recorded single-unit activity, BOLD signals and local-field potentials during rivalry. Brain imaging studies of humans experiencing binocular rivalry reveal widespread, perception-related modulations of BOLD responses, including within the lateral geniculate nucleus, V1 and higher visual areas [9]. This distribution of brain regions differs from those exhibiting target-related BOLD modulations during motion-induced blindness, implying that the two phenomena are not mediated by the same neural circuits. However, the distinct circuits producing these two phenomena may embody equivalent neural operations that lead to equally compelling fluctuations in visual perception, in which case we could reasonably hope to see the same neural footprints associated with spiking, BOLD and local-field potentials for rivalry and motion induced blindness, albeit in different brain areas.

References

1. Bonneh, Y., Cooperman, A., and Sagi, D. (2001). Motion induced blindness in normal observers. *Nature* 411, 798–801.
2. Kim, C.Y., and Blake, R. (2005). Psychophysical magic: rendering the visible “invisible”. *Trends Cogn. Sci.* 9, 381–388.
3. Wilke, M., Logothetis, N.K., and Leopold, D.A. (2006). Local field potential reflects perceptual suppression in monkey visual cortex. *Proc. Natl. Acad. Sci. USA* 103, 17507–17512.
4. Maier, A., Wilke, M., Aura, C., Zhu, C., Ye, F.Q., and Leopold, D.A. (2008). Divergence of fMRI and neural signals in V1 during perceptual suppression in the awake monkey. *Nat. Neurosci.* 11, 1193–1199.
5. Donner, T.H., Sagi, D., Bonneh, Y.S., and Heeger, D.J. (2008). Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. *J. Neurosci.* 28, 10298–10310.
6. Jack, A.I., Shulman, G.L., Snyder, A.Z., McAvooy, M., and Corbetta, M. (2006). Separate modulations of human V1 associated with spatial attention and task structure. *Neuron* 51, 135–147.
7. Scholvinck, M., and Rees, G. (2008). Neural correlates of motion-induced blindness in the human brain [Abstract]. *J. Vis.* 8, 793a. <http://journalofvision.org/8/6/793/>. DOI: 10.1167/8.6.793.
8. Libedinsky, C., Savage, T., and Livingstone, M. (2008). *Nature Precedings*: hdl:10101/npre.2008.1506.1.
9. Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. *Trends Cogn. Sci.* 10, 502–511.

1512 Wilson Hall, Vanderbilt University, Nashville, TN 37240, USA. ²Institute of Biology, Otto-von-Guericke University, 39120 Magdeburg, Germany.
E-mail: Randolph.blake@vanderbilt.edu;
Jochen.braun@ovgu.de

DOI: 10.1016/j.cub.2008.11.009

Evolutionary Cooperation: Male Cleaner Fish Aggression May Promote Female Cooperation

A new study has shown that mixed-sex pairs of cleaner fish provide a better — more cooperative — service than singletons despite pairs facing an apparent Prisoner’s dilemma.

Maxwell N. Burton-Chellew

Why would Darwinian evolution produce organisms that act to increase the success of others? The evolution of such behaviour is problematic because, at first sight, cooperative behaviours appear to be disadvantageous, and yet cooperation is witnessed throughout Nature. The most powerful and successful explanation has been Hamilton’s

theory of inclusive fitness [1,2], which explains how seemingly disadvantageous alleles can also increase their transmission *indirectly* by helping other individuals, typically close relatives, that are likely to share the same allele [1,2]. Yet cooperation also occurs between unrelated individuals and even between different species. The inherent instability of such cooperation between non-relatives is often conceptualised with the aid of

the Prisoner’s dilemma [3] or the tragedy of the commons [4], whereby individuals do best by not cooperating (cheating), no matter what their partners do. This results in an inevitable outcome (hence ‘tragic’) in which all rational actors cheat, even though they all would be better off in the long-term if they had all cooperated, hence the dilemma [3,4].

A new study by Bshary *et al.* [5] has now shown that cooperation is achieved between individuals of a cleaner reef-fish species (*Labroides dimidiatus*) that service shared clients (Figure 1), primarily because females are more cooperative towards their clients when they are working with a male than when alone. This facultative cooperation may be a response to the threat of male aggression. The nature of this cooperation provides an added twist

to a classic and challenging example of cooperation between species.

For cooperative behaviour between non-relatives to be evolutionarily stable it must be favoured by hidden direct-fitness benefits that outweigh any apparent costs and it is the job of evolutionary biologists to elucidate these [6]. Broadly speaking, such cooperation may be favoured for one or other of two reasons: because it is also directly beneficial in the long run to the performer, more so than it is costly (as, for example, in group augmentation effects [7]); or because it is enforced, through the policing [8], punishment [9–11] or sanctioning [12] of cheaters, and/or through the rewarding of cooperators, via mechanisms such as direct [13] or indirect reciprocity [14]. Such cooperation is therefore dependent on a high probability of future interactions (the ‘shadow of the future’) [3,13].

Cleaner fish benefit from eating ectoparasites, and clients benefit from being ‘cleaned’, so this relationship is arguably mutualistic; that is, both parties directly benefit from their own actions [15]. The explanation for such extraordinary behaviour can therefore appear boringly straightforward, but this fails to realise that cooperative actions are often underpinned by the tension that arises from a conflict of interests. In particular, both cleaners and clients could gain more: cleaners by eating valuable client mucus/tissue instead of parasites, and (predatory) clients by eating their cleaners afterwards. Both these behaviours, however, are damaging to the recipients. Therefore the key questions have been; how is the conflict over what the cleaner eats resolved? And why do clients not eat their cleaners? Clients that refrain from eating their cleaners then face the challenge of how to make cleaners feed against their preference in order to receive a high service quality.

Closer inspection reveals that cleaners do sometimes cheat and that this cheating depends on key ecological factors. Cleaners show facultative behaviour depending on whether clients are predators or not, and whether they are from a ‘choosy’ species or a resident species. Sensibly, predatory clients are cheated far less often than non-predatory clients [15], and choosy species are chosen ahead of resident species, which can be cleaned later [15]. Plus, cleaners are



Figure 1. A pair of cleaner wrasse, *Labroides dimidiatus* (smaller, striped fish) foraging on an *Acanthurus mata* individual (photo by Gerry Allen, courtesy of Redouan Bshary).

more cooperative when observed by choosy, as opposed to resident, clients [15]. Clients act to limit this cheating by either punishing cleaners (chasing them and biting at them) or by imposing sanctions on them (terminating the interaction and perhaps finding alternative cleaners) [15].

These dynamics suggest that cleaner fish mutualisms operate within a biological market [16], whereby reputation effects are important in determining levels of service [17] and more valuable clients receive better service. There is also an added twist because although cleaners typically act alone (singletons), they sometimes act in mixed-sex pairs comprising a male and the largest female in his harem. In their new study, Bshary *et al.* [5] found that when cleaners operate in pairs on the same client, they face a potential prisoner’s dilemma, but that this dilemma is probably resolved through enforcement (punishment). The dilemma arises because the client is liable to impose sanctions (to leave) upon both members of the pair even if only one of them cheats. Thus, if a member of a pair refrains from eating mucus, it is not only cooperating with the client, but it is also cooperating with its partner. But such cooperation is susceptible to exploitation by a less cooperative partner. This means that cleaner pairs should cheat more often, but paradoxically we know that clients prefer cleaning pairs to singletons [18].

The pressure to cheat also increases with time for both pairs and singletons, because the benefits of foraging diminish over time as parasites become depleted.

Bshary *et al.* [5] took this case of diminishing returns and modelled it with the Marginal-Value Theorem [19], which calculates the optimal time to ‘forage’ on a ‘patch’ before moving on. Traditionally the decision concerns when an animal should physically leave one patch as it becomes more and more depleted, but the model works just as well for cleaner fish, with the decision to cheat representing the decision to leave a patch (because cheating may provoke the client to leave). Thus Bshary *et al.* [5] could calculate how long an individual should wait before cheating, and found that, providing that the benefit of cheating was not too great, pairs should provide greater cleaning service to clients, providing they cooperate with each other.

The authors then looked at the natural behaviour in the field and found that pairs did indeed provide a better service, as they cheated less often overall compared to singletons. Careful observations revealed that it was primarily the females that altered their behaviour, depending upon whether they were acting alone (more likely to cheat) or within a pair (less likely). Laboratory experiments, in which instances of ‘cheating’ resulted in all

the food being withdrawn, confirmed these findings and again revealed that the feeding choices of females were conditional upon whether they were feeding alone or in a pair.

Why are females conditionally cooperative whereas males are not so inclined? Interestingly the males were observed to behave aggressively towards the females quite often after removal of the food or when the client left. This aggressive behaviour could be an evolved mechanism of punishment that causes females to be more cooperative. While the proof is missing, a previous study by Bshary and Grutter [20] showed that aggression by clients is punishment as it causes cleaners to feed more against their preference. Hence it is likely that male aggression has a similar effect. In other words, the threat of 'punishment' from males, which are larger and thus presumably have more capacity to punish, may act to reduce the benefit of cheating and thus shifts the females' optimal foraging strategy.

Bshary *et al.* [5] have therefore suggested that dominance interactions that facilitate punishment within paired members of the same species of cleaner fish may favour cooperation both between themselves and towards their clients. Their study

highlights the general finding that cooperation can be encouraged both through increased rewards for cooperating or through increased costs for not-cooperating. The latter may be the more common evolutionary outcome because the cost of punishing declines as it becomes more common, whereas the cost of rewarding cooperators increases as the trait becomes more common [10,11].

References

1. Hamilton, W.D. (1963). Evolution of altruistic behavior. *Am. Nat.* 97, 354–356.
2. Hamilton, W.D. (1964). Genetical evolution of social behaviour. *J. Theor. Biol.* 7, 1–52.
3. Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. *Science* 211, 1390–1396.
4. Hardin, G. (1968). Tragedy of commons. *Science* 162, 1243–1248.
5. Bshary, R., Grutter, A.S., Willener, A.S.T., and Leimar, O. (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature* 455, 964–966.
6. West, S.A., Griffin, A.S., and Gardner, A. (2007). Evolutionary explanations for cooperation. *Curr. Biol.* 17, R661–R672.
7. Kokko, H., Johnstone, R.A., and Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* 268, 187–196.
8. Foster, K.R., and Ratnieks, F.L.W. (2000). Social insects - facultative worker policing in a wasp. *Nature* 407, 692–693.
9. Cluttonbrock, T.H., and Parker, G.A. (1995). Punishment in animal societies. *Nature* 373, 209–216.
10. Gardner, A., and West, S.A. (2004). Cooperation and punishment, especially in humans. *Am. Nat.* 164, 753–764.
11. Lehmann, L., Rousset, F., Roze, D., and Keller, L. (2007). Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. *Am. Nat.* 170, 21–36.
12. Kiers, E.T., Rousseau, R.A., West, S.A., and Denison, R.F. (2003). Host sanctions and the legume-rhizobium mutualism. *Nature* 425, 78–81.
13. Trivers, R.L. (1971). Evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57.
14. Alexander, R.D. (1987). *The Biology of Moral Systems* (New York: Aldine de Gruyter).
15. Bshary, R., and Noë, R. (2003). Biological markets: the ubiquitous influence of partner choice on the dynamics of cleaner fish-client reef fish interactions. In *Genetic and Cultural Evolution of Cooperation*, P. Hammerstein, ed. (Cambridge, Mass., London: MIT Press in cooperation with Dahlem University Press), pp. 167–184.
16. Noe, R., and Hammerstein, P. (1994). Biological markets - supply-and-demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* 35, 1–11.
17. Bshary, R., and Grutter, A.S. (2006). Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441, 975–978.
18. Bshary, R., and Schaffer, D. (2002). Choosy reef fish select cleaner fish that provide high-quality service. *Anim. Behav.* 63, 557–564.
19. Charnov, E.L. (1976). Optimal foraging, marginal value theorem. *Theor. Pop. Biol.* 9, 129–136.
20. Bshary, R., and Grutter, A.S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biol. Lett.* 1, 396–399.

Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford OX2 6PN, UK
E-mail: max.burton@anthro.ox.ac.uk

DOI: 10.1016/j.cub.2008.11.018

Electrical Synapses: Rectification Demystified

Some electrical synapses rectify — they pass current preferentially in one direction. A new study argues that rectifying junctions result when the two sides of the junction contribute hemichannels with different properties to the gap junction.

Eve Marder

In 1959, Furshpan and Potter [1] published a landmark paper demonstrating the existence of electrical coupling between neurons in the escape system of crayfish. This paper came soon after the introduction of microelectrodes for intracellular recordings, and is often remembered as one of the earliest comprehensive studies of electrical coupling among neurons. What is often forgotten is that the junction studied by Furshpan and

Potter [1] shows rectification: that is, positive current flows preferentially in one direction, as illustrated in the simple schematic in Figure 1. What this means is that, despite the direct coupling between two neurons, information flow can nonetheless be more or less unidirectional.

While some of the computational consequences of rectifying electrical junctions have been recognized [2,3], the mechanisms giving rise to rectification at electrical synapses were largely mysterious until the recent

paper in *Current Biology* by Phelan *et al.* [4]. Electrical synapses are formed by connexins in vertebrates [5] and innexins in invertebrates [6,7], with subunits contributed to the gap junctions from both cells. Therefore, it is expected that, when gap junctions couple cells of the same type, the proteins that form the pore connecting the two cells will be molecularly identical subunits of the appropriate innexins or connexins. In this case, one would predict that current should pass symmetrically between the two cells.

In many cases in the nervous system, however, electrical synapses are found between neurons that are not of the same type [8,9]. For example, the classic studies of Furshpan and Potter [1] examined the properties of the rectifying junction between the lateral giant fiber and the motor giant neuron, and Phelan *et al.* [4] employed the escape circuit of *Drosophila* in which